CSIRO PUBLISHING
www.publish.csiro.au/journals/ajar *Australian Journal of Agricultural Research*, 2007, **58**, 648–655

Challenges and solutions for stripe rust control in the United States

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Abstract. Stripe rust of wheat, caused by *Puccinia striiformis* f. sp. *tritici*, has been one of the most destructive diseases on wheat in the western USA since the late 1950s and has become increasingly important in the central and south-eastern USA since 2000. Stripe rust of barley, caused by *P. striiformis* f. sp. *hordei*, a relatively new disease, has established and caused severe damage in the south-central and western states since the pathogen was first reported in Texas in 1991. Stripe rusts of wheat and barley have been monitored by trap nurseries and by field surveys. Collections of stripe rust from wheat, barley, triticale, and grasses have been tested on a set of 20 wheat differential genotypes for identifying races of *P. striiformis* f. sp. *tritici* and a set of 12 barley differential genotypes for identifying races of *P. striiformis* f. sp. *hordei*. In total, 62 new races of *P. striiformis* f. sp. *tritici* and 22 new races of *P. striiformis* f. sp. *hordei* have been identified since 2000. Germplasm and breeding lines of wheat and barley have been tested every year under natural infection in the field and with selected races in the greenhouse. Combinations of durable high-temperature, adult-plant resistance with effective all-stage resistance should provide more effective stripe rust control and reduce the use of fungicides.

Additional keywords: epidemiology, *Hordeum vulgare*, *Triticum aestivum*, yellow rust.

Introduction

In the USA, stripe rust of wheat, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks. (*P. s. tritici*), was first recognised in 1915 (Carleton 1915). However, the examination of herbarium specimens showed that stripe rust was collected from western Washington before 1892 (Humphrey *et al*. 1924). Stripe rust of barley, caused by *P. striiformis* f. sp. *hordei*, is a relatively new disease in the United States. The pathogen was postulated to have been introduced from Europe to Colombia in 1975 (Dubin and Stubbs 1986), and to have spread to Mexico in 1987 (Calhoun *et al*. 1988), southern Texas in 1991 (Roelfs *et al*. 1992; Marshall and Sutton 1995), and Oregon and Washington in 1995 (Chen *et al*. 1995*c*). Brown *et al*. (2001) reviewed stripe rust of barley in North America, whereas the history of research and control of stripe rust was reviewed by Line (2002) and Chen (2005). Stripe rust of wheat has been historically more destructive in the western United States (states west of the Rocky Mountains) and has become more frequently destructive in states east of the Rocky Mountains since 2000 (Chen *et al*. 2002, 2004*a*; Chen and Penman 2005, 2006). The objectives of this article are to provide an overview on epidemics and impact of stripe rusts of wheat and barley, reveal the factors contributing to the epidemics in recent years, and discuss the strategies for more effective control of stripe rust.

Stripe rust impact

The disease has caused significant damage since the first yield loss of 78 996 t, or 4% of production, in the State of Washington, was recorded in 1958 (www.cdl.umn.edu/loss.html). Destructive epidemics of wheat stripe rust occurred most often in the western USA, especially the Pacific North-west (Washington, Oregon, and Idaho). In the State of Washington, severe damage (a statewide yield loss of 5% or more, plus millions of dollars for fungicide applications) occurred in 12 of the 48 years from 1958 to 2005, all of which occurred before 1990 and most of which occurred before 1984. The most severe yield losses recorded for the State of Washington were 25% (591 108 t) in 1960 and 17% (787 236 t) in 1976. A yield loss of 8% was recorded for California in 1974. From 1975 to 1997, yield losses in California were generally low (below a state-wide yield loss of 1%). Stripe rust of wheat has once again become increasingly important in California since 1998 and in the Pacific North-west since 2002 (Chen 2005).

Although stripe rust of wheat has become more important in the South-Central States since 1984 (Line and Qayoum 1992), severe epidemics have occurred in this region and the Great Plains since 2000 (Chen *et al*. 2002; Chen 2005; Chen and Penman 2005, 2006). In 2000, wheat stripe rust occurred in more than 20 states from the Pacific North-west and California to Virginia and from Texas to North Dakota (Chen *et al*. 2002). The State of Arkansas had 7% of yield losses, the most in its recorded history. In 2001, severe stripe rust yield losses occurred in Colorado (8%), Kansas (7.3%), and Oklahoma (3.0%). In 2002, California, Arkansas, and Louisiana had 6%, 5%, and 3% yield losses, respectively. In 2003, California, Kansas, and Nebraska had 25%, 10.6%, and 10% yield losses, respectively, and Arkansas and Texas had 3% yield losses. In 2004, California, Louisiana, and Oregon had 5.0%, 4.5%, and 3.3% yield losses, respectively. Total yield losses of 250 000 t in

 10.1071/AR07045 0004-9409/07/060648

2000, 1 100 000 t in 2001, 220 000 t in 2002, 2 420 000 t in 2003, and 273 872 t in 2004 were estimated for the USA (Chen 2005; www.cdl.umn.edu/loss/loss.html). In 2005, the early occurrence of wheat stripe rust in the South-Central States and the Pacific North-west made the disease the most widely distributed, in more than 30 states, in the recorded history of the USA. The national yield losses were comparable with those in 2003, but fungicides were most widely applied in 2005 (Chen and Penman 2006).

Stripe rust of barley caused yield losses of 15, 20, 15, and 16% in 1996, 1997, 1998, and 1999, respectively, in California, 4% in Oregon in 1997, and 3% in Washington in 1998 (www.cdl.umn.edu/loss.html). Yield losses from 2000 to 2005 were less than those before 2000 in California and the Pacific North-west. However, severe damage occurred in fields growing susceptible cultivars.

Stripe rust of bluegrass, caused by *P. striiformis* f. sp. *poae*, is widely distributed in the western USA. The pathogen was also found in Minnesota in 2003. The disease is more of a problem in grass-seed production than in landscape lawns. Although selection has been used for developing resistant cultivars, application of fungicides is the major approach for controlling stripe rust in bluegrass seed production.

Races of the stripe rust pathogens

The development of races with new virulences and new combinations of previously existing virulences that circumvent resistance genes in grown cultivars is the most important factor for epidemics. Avirulence/virulence patterns of stripe rust races were determined by their reactions on a set of selected differential genotypes. Differential sets have undergone changes in number and genotypes to improve the description of avirulence/virulence patterns without losing consistency. Currently, the differential set for identifying races of *P. striiformis* f. sp. *tritici* consists of 20 wheat genotypes (Table 1) (Chen *et al*. 2002, 2004*b*; Chen 2005) and the differential set for identifying races of *P. striiformis* f. sp. *hordei* consists of 12 barley genotypes (Table 2) (Chen 2004). One hundred and twenty-one races of *P. striiformis* f. sp. *tritici* were identified from the 1960s to 2005 (Table 3) (Line and Qayoum 1992; Chen *et al*. 2002, 2004*b*; Line 2002; Chen 2005; Chen and Penman 2005, 2006) and 74 races of *P. striiformis* f. sp. *hordei* were identified from 1991 to 2005 (Table 4) (Chen *et al*. 1995*c*; Line 2002; Chen 2004; Chen and Penman 2005, 2006).

In 2000, because of the first discovery of virulence on wheat genotypes with the *Yr8* and *Yr9* resistance genes in the USA, 4 genotypes, the *Yr8* and *Yr9* near-isogenic lines in the Avocet S background, Clement, and Compair, were added to the 16 genotypes previously used to differentiate races of *P. striiformis* f. sp. *tritici* in the USA (Chen *et al*. 2002). From samples collected from 20 states, 21 previously identified and 21 new races were identified. Of the 21 new races, 8 had new combinations of previously existing virulences, and 13 had

Table 1. Wheat genotypes used to differentiate races of *Puccinia striiformis* f. sp. *tritici* in the United States

Differential[A] No.	Name	Genotype ID number[B]	Type	*Yr* gene[C]	Year added to differential set
1	Lemhi	CI 011415	Spring	*Yr21*	1968
2	Chinese 166	CI 011765	Winter	*Yr1*	1968
3	Heines VII	PI 201195	Winter	*Yr2*,*YrHVII*	1968
4	Moro	CI 013740	Winter	*Yr10*,*YrMor*	1968
5	Paha	CI 014485	Winter	*YrPa1*,*YrPa2*,*YrPa3*	1974
6	Druchamp	CI 013723	Winter	*Yr3a*,*YrD*,*YrDru*	1969
7	Rie. 47-51/*Yr5*[D]	YR 00004	Spring	*Yr5*	2004
8	Produra	CI 017460	Spring	*YrPr1*,*YrPr2*	1974
9	Yamhill	CI 014563	Winter	*Yr2*,*Yr4a*,*YrYam*	1974
10	Stephens	CI 017596	Winter	*Yr3a*,*YrS*,*YrSte*	1976
11	Lee	CI 012488	Spring	*Yr7*,*Yr22*,*Yr23*	1977
12	Fielder	CI 017268	Spring	*Yr6*,*Yr20*	1980
13	Tyee	CI 017773	Winter	*YrTye*	1983
14	Tres	CI 017917	Winter	*YrTr1*,*YrTr2*	1989
15	Hyak	PI 511674	Winter	*Yr17*	1990
16	Express	PI 573003	Spring	Unknown	1998
17	*Yr8*[D]	YR 000008	Spring	*Yr8*	2000
18	*Yr9*[D]	YR 000009	Spring	*Yr9*	2000
19	Clement	PI 518799	Winter	*Yr9*,*YrCle*	2000
20	Compair	PI 325843	Spring	*Yr8*,*Yr19*	2000

[A] Riebesel 47–51 (*Yr9*), a winter wheat, was used as differential no. 7 before 2004, but was replaced by the *Yr5* near-isogenic line. Riebesel 47–51 was resistant (IT 0) to all races detected before 2000, but it had IT 0, 2, 3, 4, 5, 6, and 7 when tested with races detected after 2000. Urediniospores collected from Riebesel 47–51 with ITs 4 to 7 produced lower ITs and eventually were unable to produce spores. This change of differential no. 7 did not change the description of avirulence and virulence for all described races.

[B] CI, Crop index number; PI, plant identification number; and YR, yellow rust resistance gene line number.

[C] Refer to Chen and Line (1992*a*, 1992*b*, 1993), Chen *et al*. (1995*a*, 1995*b*, 1998), and McIntosh *et al*. (1998) for the *Yr* genes.

[D] *Yr5*, *Yr8*, and *Yr9*, developed by the Plant Breeding Institute, University of Sydney, Australia, are near-isogenic lines in the 'Avocet Susceptible' background (Wellings *et al*. 2004).

Table 2. Barley genotypes used to differentiate races of *Puccinia striiformis* f. sp. *hordei*

No.	Differential genotype		Resistance gene[A]
	Name	ID number	
1	Topper	–	–
2	Heils Franken	PI 290183	*Rps4*, *rpsHF*
3	Emir	CIho 13541	*rpsEm1*, *rpsEm2*
4	Astrix	CIho 13862	*Rps4*, *rpsAst*
5	Hiproly	CIho 03947	*rpsHi1*, *rpsHi2*
6	Varanda	PI 410865	*rpsVa1*, *rpsVa2*
7	Abed Binder 12	PI 327961	*rps2*
8	Trumpf	PI 548762	*rpsTr1*, *rpsTr2*
9	Mazurka	PI 399501	*Rps1.c*
10	Bigo	CIho 11795	*Rps1.b*
11	I 5	PI 288187	*Rps3*, *rpsI5*
12	Bancroft	PI 605474	Not determined

[A]Chen and Line (2003).

virulences to one or more of the lines *Yr8*, *Yr9*, Clement, and Compair (Table 3). The new group of races represented by PST-78 (virulent to Lemhi, Heines VII, Lee, Fielder, Express, *Yr8*, *Yr9*, Clement, and Compair) has overcome resistance in many cultivars with resistance controlled by *Yr6*, *Yr7*, and *Yr9*. This group of races has spread throughout the USA and Canada, and has continued evolving into new races through addition or deletion of one or more of the virulences. The development and spread of this group of races have caused the devastating epidemics since 2000.

In 2001, 21 previously identified races and 10 new races were identified from samples from the USA and Canada (Table 3). The most predominant races were PST-78 (23.4%) and PST-80 (17.4%, the same virulences of PST-78 plus virulence to Produra), which were first detected in 2000. A new race, PST-90, which has a combination of virulence on Tres (*YrTr1*, *YrTr2*) and virulences of PST-78, was detected in states east of the Rocky Mountains from Texas to Minnesota.

In 2002, 30 previously identified races and 9 new races were identified (Table 3). Race PST-78 was the most predominant race, accounting for 31.1% of all isolates. This race spread to the Pacific North-west and caused a severe epidemic mainly on spring-wheat cultivars, such as Zak and Jubilee, which do not have durable high-temperature, adult-plant (HTAP) resistance (Chen *et al*. 2003). The new group of races with common virulence to Lemhi, Heines VII, Lee, Fielder, *Yr8*, *Yr9*, Clement, and Compair accounted for 75% of all samples. New races that have virulence to more differential genotypes and commercial cultivars were detected. For example, race PST-97 has all virulences of PST-78 plus virulence to Stephens (*Yr3a*, *YrSte*, *YrSte2*), PST-98 has all virulences of PST-80 plus virulence to Stephens, and PST-99 has all virulences of PST-78 plus virulences to both Stephens and Yamhill (*Yr2*, *Yr4a*, *YrYam*) (Chen 2005).

In 2003, from more than 400 samples that were collected from 25 states, 24 previously identified races and 10 new races were identified (Table 3) (Chen *et al*. 2004*b*). Races PST-98 (29.4%) and PST-100 (33.1%) were the most predominant, while the frequencies of PST-78 and PST-80 that were predominant in 2001 and 2002 decreased to 5.6% and 4.8%. More than 90% of all samples belonged to the group of races with virulences to Lemhi, Heines VII, Lee, Fielder, Express, *Yr8*, *Yr9*, Clement, and Compair. The change in predominant races from PST-78 and PST-80 to PST-98 (virulent on Lemhi, Heines VII, Produra, Stephens, Lee, Fielder, Express, *Yr8*, *Yr9*, Clement, and Compair) and PST-100 (virulences of PST-98 plus virulence to Yamhill) was probably due to the virulences to Yamhill and seedlings of Stephens, which are cultivars grown in California and the Pacific North-west and also used as parental genotypes in many other cultivars. A new race, PST-102, which combines the virulence to Tres and the virulences of PST-100, was detected at a low frequency (Chen 2005).

In 2004, of a total of 28 PST races detected, 6 were new (Table 3) (Chen and Penman 2005). Race PST-100, accounting for 50% of all samples, was the most predominant, followed by PST-102 (17.7%). More than 90% of the PST isolates belonged to the group of races with virulences to *Yr8*, *Yr9*, and other resistance genes, which caused widespread stripe rust epidemics in the USA from 2000 to 2004. Five of the 6 new races belonged to this group. Major changes in virulence were the appearance of new races PST-111 (with the virulence to Paha and the virulences of PST-100), PST-115 (with the virulence to Paha and the virulences of PST-102), and PST-114 (with the virulence to Moro and the virulences of PST-102) (Chen and Penman 2005).

In 2005, stripe rust samples of 473 from wheat, 3 from triticale, and 7 from various grasses were identified as *P. striiformis* f. sp. *tritici* races (Chen and Penman 2006). Of a total of 27 identified races, 6 were new (Table 3). The most predominant races included PST-115, PST-100, and PST-102. Some new races combined virulences to Moro, Paha, and the virulences of PST-100. The increase in frequencies of PST-115 and the appearances of new races, especially race PST-116 (virulent on Lemhi, Heines VII, Moro, Paha, Produra, Yamhill, Stephens, Lee, Fielder, Express, *Yr8*, *Yr9*, Clement, and Compair), circumvented resistance in several cultivars of hard red, hard white spring, and soft white wheat grown in the Pacific North-west. The *Yr5* near-isogenic line, which was first included in the differential set in 2004, remained resistant. The *Yr15* near-isogenic line, which is not used as a differential genotype, was resistant in all field locations tested throughout the USA.

The phenomenon that races of *P. striiformis* f. sp. *tritici* with broader spectra of virulences have become more and more predominant can be explained by their capability of infecting and reproducing on more grown cultivars. The phenomenon may also be explained by results of a recent study by Milus and Seyran (2004), which indicated that some recent races had a relatively short latent period at a high temperature (18°C) compared with old races before 2000.

The USA population of *P. striiformis* f. sp. *hordei* has continued evolving since the first report of this pathogen in 1991. Before 2000, 52 races had been described (Chen and Line 2001) and from 2000 to 2005, 22 new races have been identified (Table 4). Before 2001, 11 barley genotypes (Topper, Heils Franken, Emir, Astrix, Hiproly, Varunda, Abed Binder 12, Trumpf, Mazurka, Bigo, and I 5) were used as differentials. Bancroft, the first barley cultivar that was developed particularly for resistance to stripe rust (Wesenberg *et al*. 2001), was added to the differential set in 2001. Beginning in 1997, races with a narrow spectrum of virulence tended to predominate. In 2000,

Table 3. Races of *Puccinia striiformis* f. sp. *tritici*, virulence descriptions, and year first detected in the United States

PST race	Virulences to differentials[A]	Year first detected	PST race	Virulences to differentials[A]	Year first detected
1	1,2	1963	62	1,2,12,16	2000
2	1,2,5	1964	63	1,8,12,16	2000
3	1,3	1964	64	1,2,11,12,16	2000
4	1,3	1968	65	1,8,10,12,16	2000
5	1,3,4	1972	66	1,2,10,11,12,16	2000
6	1,6,8,12	1974	67	1,2,3,11,12,16	2000
7	1,3,5	1974	68	1,3,12,16,17	2000
8	1,3,9	1975	69	1,2,11,12,16,18	2000
9	1,3,6,8,12	1976	70	1,3,11,12,16,18	2000
10	1,2,3,9	1976	71	1,8,10,12,18,19	2000
11	1	1976	72	1,6,8,10,12,18,19	2000
12	1,5,6,12	1976	73	1,2,3,11,12,16,18,19	2000
13	1,5,6,8,12	1976	74	1,8,10,12,17,18,19	2000
14	1,8,12	1976	75	1,4,8,10,12,17,18,19	2000
15	1,3,6,8,10	1977	76	1,2,12,16,17,18,20	2000
16	1,3,9,11	1977	77	1,11,12,16,17,18,19,20	2000
17	1,2,3,9,11	1977	78	1,3,11,12,16,17,18,19,20	2000
18	1,3,4,9	1977	79	1,8,11,12,16,17,18,19,20	2000
19	1,3,6,8,10,12	1977	80	1,3,8,11,12,16,17,18,19,20	2000
20	1,6,8,10,12	1978	81	1,14	2001
21	2	1980	82	1,11,17	2001
22	1,3,12	1981	83	1,3,6,11	2001
23	1,3,6,9,10	1981	84	1,8,10,12,18	2001
24	1,3,5,12	1981	85	1,8,10,12,17,18	2001
25	1,3,6,8,9,10,12	1982	86	1,8,10,12,16,18,19	2001
26	1,3,9,12	1983	87	1,2,11,12,16,17	2001
27	1,3,12,13	1983	88	1,11,12,16,17,20	2001
28	1,3,4,12	1983	89	1,12,16,17,18,19,20	2001
29	1,3,4,5	1983	90	1,3,11,12,14,16,17,18,19,20	2001
30	1,4,6,8,12	1983	91	1,9,10	2002
31	1,3,5,11	1983	92	1,10,12	2002
32	1,4	1984	93	1,6,10,12	2002
33	1,3,9,12,13	1984	94	1,9,10,12	2002
34	1,3,4,5,12	1985	95	1,4,8,10,12,14	2002
35	1,10	1985	96	1,4,6,8,10,12,14	2002
36	1,3,4,9,12	1987	97	1,3,10,11,12,16,17,18,19,20	2002
37	1,3,6,8,9,10,11,12	1987	98	1,3,8,10,11,12,16,17,18,19,20	2002
38	1,3,11	1987	99	1,3,9,10,11,12,16,17,18,19,20	2002
39	1,2,4	1989	100	1,3,8,9,10,11,12,16,17,18,19,20	2003
40	1,4,14	1989	101	1,2,3,8,9,10,11,12,16,17,18,19,20	2003
41	1,3,4,14	1989	102	1,3,8,9,10,11,12,14,16,17,18,19,20	2003
42	1,3,11,12	1990	103	1,9,10,11,12,16,17,18,19,20	2003
43	1,3,4,5,12,14	1990	104	1,2,3,9,10,11,12,16,17	2003
44	1,4,5	1990	105	1,8,10,11,12,16,17,20	2003
45	1,3,12,13,15	1990	106	1,8,10,11,12,16,17	2003
46	1,3,6,9,10,11	1991	107	1,3,4,5,9,10,14	2003
47	1,6,8,12,13	1992	108	1,3,4,6,9,10,12	2003
48	1,6,8,12,13,14	1992	109	1,4,8,10,12	2003
49	1,3,11,14	1992	110	1,3,8,9,11,12,16,17,18,19,20	2004
50	1,3,4,5,14	1992	111	1,3,5,8,10,11,12,16,17,18,19,20	2004
51	1,3,4,12,14	1992	112	1,2,8,10,11,12,16,17,18,19,20	2004
52	1,4,8,12,14	1993	113	1,2,3,8,9,10,11,12,14,16,17,18,19,20	2004
53	1,6,10	1994	114	1,3,4,8,9,10,11,12,14,16,17,18,19,20	2004
54	1,3,4,6,8,9,10,12	1994	115	1,3,5,8,9,10,11,12,14,16,17,18,19,20	2004
55	1,6,10,11	1994	116	1,3,4,5,8,9,10,11,12,14,16,17,18,19,20	2005
56	1,4,6,8,12,14	1995	117	1,3,6,8,9,10,11,12,14,16,17,18,19,20	2005
57	1,3,4,6,8,10,12	1996	118	1,3,8,9,10,11,12,13,14,16,17,18,19,20	2005
58	1,11,12,16	1998	119	1,3,4,8,9,10,11,12,16,17,18,19,20	2005
59	1,3,11,12,16	1998	120	1,3,4,11,12,14,16,17,18,19,20	2005
60	1,12,16	2000	121	1,8,10,12,17,18,19,20	2005
61	1,4,10,12	2000			

[A] See Table 1 for the number and name of each differential genotype.

Table 4. Races of *Puccinia striiformis* f. sp. *hordei* (PSH), virulence descriptions, and year first detected in the United States

PSH race	Virulence description[A]	First year detected	PSH race	Virulence description[A]	First year detected
1	1,2	1993	38	1,2,3,4,5,7,8	1996
2	1,2,3	1994	39	1,3,7,8	1996
3	1,2,4	1993	40	1,2,3,4,7,9	1996
4	1,2,5	1993	41	1,3,4,6,7,9	1996
5	1,6,7	1994	42	1,4,5,7,9	1996
6	1,2,3,4	1993	43	1,4,8	1996
7	1,2,4,5	1993	44	1,3,7	1996
8	1,2,3,7	1994	45	1,3,4,6,7,8	1996
9	1,2,3,4,6	1993	46	1,7,8	1996
10	1,3,5,6,7	1994	47	1,3,4,5,7	1996
11	1,3,6,7,8	1993	48	1	1997
12	1,2,3,4,5,8	1993	49	1,2,3,4,5,6,7,8,9,10,11	1997
13	1,2,3,6,8,9,10	1994	50	1,5	1998
14	1,2,3,4,5,6,7,8	1993	51	1,5,7	1998
15	1,3,4,7,8	1995	52	1,5,7,8	1998
16	1,3,5,7,8	1995	53	1,8,9	2001
17	1,2,4,5,7,8	1995	54	1,7,8,12	2001
18	1,3,4,5,7,8	1995	55	1,8,9,12	2001
19	1,3,5,6,7,8	1995	56	1,5,7,8,12	2001
20	1,3,6,7,8,9	1995	57	1,7,8,9,10	2001
21	1,3,4,7,8,9,10	1995	58	1,7,8,10,12	2001
22	1,4,7,8,9,10	1995	59	1,7,8,11,12	2001
23	1,2,3,4,7,8,9	1995	60	1,5,7,8,9,10,12	2001
24	1,3,4,5,6,7,8	1995	61	1,3,7,12	2002
25	1,3,4,5,7,8,9	1995	62	1,3,7,8,12	2002
26	1,2,3,4,5,7,8,9	1995	63	1,3,5,7,8,12	2002
27	1,3,5,6,7,8,9,10	1995	64	1,5,7,8,10,12	2002
28	1,2,3,4,5,6,7,8,9	1995	65	1,2,3,4,7,8,12	2002
29	1,2,3,4,5,6,7,8,10	1995	66	1,3,6,7,8,11,12	2002
30	1,3,4,5,6,7,8,9,10	1995	67	1,3,5,6,7,8,11,12	2002
31	1,2,3,4,5,6,7,8,9,10	1995	68	1,6,7,8,10,12	2003
32	1,3,5	1996	69	1,5,6,7,8,9,10,11,12	2003
33	1,7	1996	70	1,7,10,12	2004
34	1,7,8,9	1996	71	1,3,5,6,7,8,9,10,12	2004
35	1,4,7	1996	72	1,2,3,4,5,6,7,8,9,10,11,12	2004
36	1,4	1996	73	1,5,7,8,9	2005
37	1,2,4,7	1996	74	1,5,7,12	2005

[A]See Table 2 for the barley genotypes used to differentiate races of *P. striiformis* f. sp. *hordei*.

seven races, all of which had been previously identified, were detected from the samples collected from California, Idaho, Oregon, and Washington. None of the 7 races was virulent on more than 4 differential genotypes. In 2001, of a total of 19 races identified from samples from Texas, California, Oregon, and Washington, 8 races were new. The most predominant races were PSH-46 (virulent to Topper, Abed Binder 12, and Trumpf), PSH-54 (virulent to Topper, Abed Binder 12, Trumpf, and Bancroft), and PSH-56 (virulent to Topper, Hiproly, Abed Binder 12, Trumpf, and Bancroft), accounting for 13.8, 19.0, and 13.8% of total collections, respectively. Races virulent on 2–4 of the 12 differential genotypes accounted for 56.8% of the isolates. The most virulent races, PSH-14 (virulent to Topper, Heils Franken, Emir, Astrix, Hiproly, Varunda, Abed Binder 12, and Trumpf) and PSH-26 (virulent to Topper, Heils Franken, Emir, Astrix, Hiproly, Abed Binder 12, Trumpf, and Mazurka), had isolation frequencies of 1.7% to 3.4%, respectively. In 2002, from barley stripe rust samples from California, Oregon, and Washington, 14 races were detected, 7 of which were new. PSH-56 (31.4%) and PSH-54 (20.0%) remained the most predominant races. In 2003, in total 9 races were detected, of which 2 were new (Chen *et al*. 2004*b*). Races PSH-54, PSH-56, PSH-48 (only virulent to Topper of the 12 differentials), and PSH-33 (virulent to Topper and Abed Binder 12) had isolation frequencies of 27.8, 16.7, 16.7, and 13.9%, respectively. All other races had frequencies less than 5.0%. In 2004, in total 15 races were detected from samples from California, Idaho, Oregon, and Washington, and 3 of the 15 races were new (Chen and Penman 2005). One of the new races, PSH-72, was virulent to all 12 differential barley genotypes. Even though races predominant in previous years, such as PSH-56, were commonly detected, a new race, PST-71, virulent to Topper, Emir, Hiproly, Varunda, Abed Binder 12, Trumpf, Mazurka, Bigo, and Bancroft, was most common. In 2005, samples of barley stripe rust were collected from California, Oregon, Washington, Idaho, and Montana; 7 previously identified and 2 new races were identified

from samples tested. Race PST-52 (virulent to Topper, Hiproly, Abed Binder 12, and Trumpf) was the most predominant race (Chen and Penman 2006).

Compared with *P. striiformis* f. sp. *tritici*, races of *P. striiformis* f. sp. *hordei* with a relatively narrow spectrum of virulence have tended to be more predominant. This phenomenon can be explained by the relatively low selection pressure from the barley cultivars. In California and the Pacific North-west, where barley stripe rust mainly occurs, barley cultivars are either susceptible or have non-race-specific high-temperature, adult-plant (HTAP) resistance. Races with a narrow spectrum of virulence may have advantages in aggressiveness over those with a wide spectrum of virulence on susceptible cultivars or cultivars with a moderate level of non-race-specific HTAP resistance, such as the most widely grown cv. Baronesse.

Control of stripe rust using plant resistance

Stripe rust can be best controlled by growing resistant cultivars. Two major types of resistance, all-stage resistance and HTAP resistance, have been used in developing cultivars resistant to stripe rust. All-stage resistance, also called seedling resistance, can be detected at the seedling stage, but usually provides high-level resistance to specific races throughout all growth stages. The high level, and easy incorporation into commercial cultivars due to simple inheritance, made all-stage resistance more attractive to breeding programs and its contribution to stripe rust control. However, every severe epidemic was caused by the failure of all-stage resistance in widely grown cultivars. Multi-line cultivars and gene pyramiding, which can greatly expand the life span of all-stage resistance, have been successfully used in the USA to control stripe rust. The multi-line cv. Rely, which was composed of 10 individual lines in the 'Tres' background with more than 10 different resistance genes, has maintained excellent resistance since it was released and widely grown in the Pacific North-west in 1991 (Allan *et al*. 1993; Chen 2005). As an approach for developing resistant cultivars, gene pyramiding has been used for much longer than generally realised. Most cultivars grown in the USA, especially in the western USA, have more than one gene for stripe rust resistance. However, the early gene pyramiding was generally through addition of a gene or genes to resistance genes that had been overcome by virulent races. Such gene addition might expand the resistance through the effectiveness of the added gene or genes and/or through complementary interactions of genes that might be ineffective separately. Recently, gene pyramiding has become a more directed approach. Combining genes that are individually effective against the stripe rust population will likely make resistance last longer. The current effort in gene pyramiding, effective genes for all-stage resistance using molecular markers in many breeding programs, should result in new cultivars with relatively durable resistance.

The USA wheat breeders and pathologists started to recognise and use adult-plant resistance in the 1950s. Against general public and scientific concepts of resistance, Vogel (1964) was the first in developing cultivars with non-race-specific stripe rust resistance in the 1950s. 'Gaines', which had a level of resistance better than susceptible cultivars in the adult-plants, was released in 1961 (Vogel 1964); 'Nugaines', which had improved resistance in adult plants, was released in 1965 (Vogel and Peterson 1974). Because of its good plant type and lack of known seedling resistance genes, Nugaines is used in the greenhouse to increase spores from stripe rust collections for identifying races of *P. striiformis* f. sp. *tritici*. Although the levels may not be adequate, the resistances in Gaines and Nugaines have not been changed by any race for more than 40 years.

The USA wheat scientists have long recognised the temperature effects on resistance (Sharp 1965; Lewellen *et al*. 1967; Brown and Sharp 1969). Line *et al*. (1974) and Qayoum and Line (1985) described HTAP resistance. Seedlings of cultivars with only HTAP resistance are susceptible to all races of *P. striiformis* f. sp. *tritici* at both low and high temperatures. Adult-plants of HTAP resistant cultivars are susceptible at low temperatures, but resistant at high temperatures. To identify cultivars with HTAP resistance, we use gradually changing diurnal temperatures, 4–20°C (low temperatures) and 10–35°C (high temperatures), which simulate the natural temperatures in the early and late growth stages, for the seedling and adult-plant tests, respectively. The concept of HTAP resistance has had a profound effect on the breeding programs for developing stripe rust resistant cultivars. The major wheat cultivars grown in the USA Pacific North-west and some cultivars in the Great Plains have durable resistance. Because HTAP resistance is generally controlled by quantitative trait loci (Milus and Line 1986*a*, 1986*b*; Chen and Line 1995*a*, 1995*b*), it is relatively difficult to incorporate into commercial cultivars compared with single-gene controlled all-stage resistance. Molecular markers are currently being developed for more efficient incorporation and combination of genes for HTAP resistance into new cultivars.

Because HTAP resistance is more effective when stripe rust infection occurs in the late growth stages and under high temperatures, this type of resistance, depending upon levels of resistance, may not be adequate in regions where stripe rust infects seedlings that continue developing during the winter, and when the weather is cool during the late growth stages. In the USA, a combination of HTAP resistance and effective all-stage resistance is the best approach to develop durable and high-level resistance.

Control of stripe rust with fungicides

In the USA Pacific North-west, chemical control of stripe rust was attempted in the 1950s and 1960s. However, the economical and successful use of fungicides was not reported until the late 1970s. The first large-scale and effective use of fungicides to control stripe rust was in 1981. Triadimefon (Bayleton®) was widely used as a foliar fungicide in the Pacific North-west, which prevented multi-million dollar losses (Line 2002). Through intensive testing, triadimenol (Baytan®) was registered in the 1980s as a seed-treatment fungicide to control early development of stripe rust (Rakotondradona and Line 1984; Scott and Line 1985).

The USDA-ARS cereal rust program at Pullman, Washington, has conducted fungicide tests every year since the 1970s. The test results have been reported annually in 'Fungicide and Nematicide Tests' before 2007 and in 'Plant Disease Management Reports (PDMR)' (www.plantmanagementnetwork.org/pub/trial/pdmr/) since 2007. Through the efficacy evaluation of

fungicides, several fungicides have been registered for use on wheat and barley to control stripe rust. Five fungicides, Tilt® (propiconazole), Quadris® (azoxystrobin), Stratego® (propiconazole + trifloxystrobin), Headline® (strobilurin), and Quilt® (azoxystrobin + propiconazole), are currently registered. The program also tested wheat and barley cultivars for their responses to fungicide application in annual field nurseries under natural stripe rust infection. The test data were used to estimate yield losses caused by stripe rust and determine yield increase by fungicide application. The data were used, together with yield potential, disease pressure, and grain price, to guide growers to make decisions for using or not using fungicides on particular cultivars. Subsequently, timely and appropriate use of fungicides on cultivars with different types and various levels of resistance has maximised profits and reduced unnecessary use of fungicides.

In recent years, fungicide tests have been conducted in other states to provide guidelines for timely application of fungicides (Cartwright *et al*. 2001; Fichtner *et al*. 2002; Colyer and Vernon 2003, 2004, 2005; Padgett and Rea 2003; Padgett *et al*. 2004, 2005; Purvis *et al*. 2005). The wide application of foliar fungicides has greatly reduced yield losses since 2000 in the USA. In Texas, foliar application of fungicides to control stripe rust increased yield by 41% and increased 1000-kernel weight by 33% above fields without fungicide application in 2004 (Reid and Swart 2004). In the state of Washington alone, use of foliar fungicides to control stripe rust saved wheat growers 15–30 million dollars at a cost of 2–4 million dollars every year from 2002 to 2005 (Chen 2005).

Although economical control of stripe rust has been achieved with timely use of effective fungicides, the cost of fungicides and their application creates a huge burden for growers. In addition, wide use of fungicides may create selection pressure for fungicide-tolerant strains of the pathogen, and may also create environmental and health problems. In regions where yield is low, fungicide may not be profitable. Although cultural practices, such as late planting, reduced irrigation, avoidance of excessive nitrogen use, and elimination of volunteer and grass plants can reduce stripe rust severities, these are either not profitable, conflicting with conservation farming, or reduce yield potential. Therefore, breeding for cultivars with durable and adequate-level resistance for every market class of wheat and barley crops in every region where stripe rust is a potential problem is the best approach to control this vastly damaging disease.

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Manuscript received 5 February 2007, accepted 17 April 2007